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RESEARCH ARTICLE

Temporal and spatial distribution patterns of dipteran assemblages in common teasel (*Dipsacus fullonum* L.) phytotelmata: Insights from eastern Slovakia

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Abstract

The common teasel (*Dipsacus fullonum* L.) represents a unique and almost unknown aquatic ecosystem referred to as phytotelma, identified almost a century ago by Varga in 1928. The present study investigates the ecology of dipterans inhabiting the phytotelmata of the teasel in eastern Slovakia. The research, conducted from May to August (11.5.2016 – 16.8.2016), focused on the temporal and spatial distribution of organisms, mainly *Dasyhelea* spp. (Ceratopogonidae) and *Metriocnemus eurynotus* (Holmgren, 1883) (Chironomidae), in the phytotelmata. A total of 1429 dipteran individuals from six families were identified, with *Dasyhelea* spp. and *M. eurynotus* dominating the samples. The temporal and spatial dynamics of the larval and pupal stages were observed. *M. eurynotus* occurred mainly in the lower levels early in the season and *Dasyhelea* entered the higher levels during the *M. eurynotus* abundance decline. Unexpectedly, *Dasyhelea* pupae were observed actively moving out of the water on the plant stems between phytotelmata levels. The study highlights the simplicity and extremity of the teasel aquatic environment and provides insights into ecological processes, such as distribution, colonisation and species interactions within the teasel ecosystem. The results contribute to the broader understanding of phytotelma ecology and highlight the importance of the common teasel as a unique habitat for dipteran communities.

Keywords

Dasyhelea, *Dipsacus*, Diptera, *Metriocnemus*, phytotelmata, teasel.

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PENSOFT

Introduction

The common teasel (*Dipsacus fullonum* L., syn. *sylvestris*) is a naturally occurring plant in Europe and relatively commonplace in Slovakia. Despite its occurrence, it hides an almost unknown aquatic ecosystem called phytotelma (plural – phytotelmata) by Varga (1928). Common teasel as a biennial plant survives the first year and winter in the form of a basal rosette of leaves (Jurica 1921). Subsequently, in spring, the rosette begins to grow in height, sometimes reaching up to 2 m (Gucker 2009). Leaves emerge on the main stem and, depending on conditions, occasionally leafy lateral branches arise (Daddario et al. 2021). The arrangement of the leaves is opposite and clustered, forming a cup for water retention, providing a temporary aquatic habitat (Jurica 1921). The volume of phytotelmata depends on leaf size and vertical position, with the average volume often being less than 100 ml. In rare cases, plants with large and wide leaves can reach a volume of more than 1000 ml of water per leaf axil (own observation). Towards the end of summer, teasel leaves begin to desiccate, losing their ability to retain water. Plants dry out and die after flowering (Gucker 2009). Phytotelmata of teasel are temporally limited, existing for 3 to 4 months depending on conditions (from May to August) (Fogašová et al. 2022). The main significant limiting factor is the weather. As an aquatic environment, phytotelmata are dependent on precipitation (Maguire 1971; Ramos and do Nascimento Moura 2019). Due to the considerable height of the plants and direct exposure to sunlight, water evaporates quickly (Baumgartner 1986; Krupa and Thomas 2019). The periodicity of the dry phase makes the survival in this ecosystem unpredictable and challenging (Zotz and Laube 2005; Williams 2006).

Information about the biota inhabiting this unique ecosystem has been documented several decades ago (Zavřel 1941; Münchberg 1955; Maguire 1959; Borobev 1960; Kitching 2001; Oboňa et al. 2024). Phytotelmata contain species representing many of the major aquatic insect orders, with true flies (Diptera) being the most common (Williams 1987). In temperate zones, phytotelmata are relatively uncommon compared to the tropical (Maguire 1971; Kitching 2000), where phytotelmata are common on Bromeliaceae or Nepenthaceae. The most common type of telmata in temperate zones are dendrotelmata (Kitching 1971), which have been studied a little more, but these are not as extreme environments when compared to phytotelmata. In contrast to *Dipsacus*, dendrotelmata are characterised by longer-lasting tree cavities, which provide a more stable microclimate in the forest compared to open grasslands, thus extending the duration of the aquatic phase. Organisms can survive the winter and their life cycles are not strictly limited in time (Gossner and Petermann 2022).

Another important difference is that between the quality and quantity of food resources (decaying wood or leaf litter) (Schmidl et al. 2008; Magyar et al. 2017). These basic characteristics and differences highlight that the aquatic environment of teasel is simpler, but indeed extreme. Phytotelmata on teasel plants, due to their simplicity,

are useful for the study of ecological processes such as distribution, colonisation and species interactions.

The main aim of this study is to describe dipteran assemblages and to find out how these ecological processes work.

Material and Methods

The study area comprised fields near the village of Demjata, located in eastern Slovakia at coordinates 49°06'31.6"N, 21°18'54.4"E. Notably, there were ten discrete clusters of teasel occurrences near the village, as shown in Fig. 1. The most distant sites were approximately 3 km apart.

As a native plant in Slovakia, teasel most often grew in small clusters near gravel roads, field margins or unmanaged meadows. The field experiment in 2016 lasted from May, when teasels started to increase in height from a leaf rosette until August when the leaves started to dry out. Nine sampling events took place at approximately 10-day intervals. Water sampling took place on the following specific dates: 1. – 11.5.2016; 2. – 21.5.2016; 3. – 31.5.2016; 4. – 9.6.2016; 5. – 17.6.2016; 6. – 26.6.2016; 7. – 5.7.2016; 8. – 3.8.2016; 9. – 16.8.2016. Sampling dates in May (1 – 3), June (4 – 6) and early July (7) were dependent on favourable conditions characterised by the presence of water in the leaf axils. Dry weather dictated a single sampling date in July and subsequent

Figure 1. Location of the sampling sites (Google Earth).

dates were carried out in August (8 – 9). A total of 90 plants were randomly selected, with ten specimens selected for examination on each sampling date. One plant with water present in the leaf axils was sampled from each site.

When randomly selecting plants, we excluded plants with all phytotelmata in the dry phase, plants with numerous damaged leaves and avoided phytotelmata with spiders present, whose webs may prevent flying insects from accessing the phytotelmata and subsequently laying eggs. During sampling, water was extracted from all phytotelmata on each studied plant using a 150 ml syringe and the entire volume was transferred to sterile plastic containers and fixed. Tweezers were used to remove organisms from leaves that were not extracted with the syringe. All plastic containers were labelled to indicate the volume of water collected and the position of the leaf axils on the stem. The position of the phytotelmata was labelled with letters from A to H, with A indicating the lowest position near the ground, with subsequent letters indicate progressively higher positions on the stem.

In the laboratory, aquatic dipteran larvae were sorted from randomly drowned insects and snails present in the samples. Diptera larvae were then identified to the lowest possible taxonomic level using a binocular stereomicroscope (with max. 50× magnification) and the identification keys of Rozkošný (1980) and Nilsson (1996). The identified specimens were then fixed in alcohol. For the fixed dominant taxa, larval body length (without head) and total pupal length were measured. Only intact specimens were measured. The data obtained were visualised in PAST (version 4.16; Hammer et al. 2001). Spindle plots were used to represent the frequency of larval size groups, where the frequency of individuals of each size group is expressed by the width of the box. The matrix plot expresses the spatio-temporal distribution of larvae.

Results

During the sampling period, a total of approximately 6.5 litres (6427.5 ml) of water was collected from the phytotelmata of the model teasel plants. A comprehensive analysis identified 1429 individuals belonging to six families of the order Diptera. The most abundant taxa included *Dasyhelea* spp. (Fig. 2) of the family Ceratopogonidae with 856 individuals and *Metriocnemus eurynotus* Holmgren, 1883 (Fig. 3) of the family Chironomidae with 546 individuals. Less abundant families included Cecidomyiidae (20 individuals), Stratiomyidae, Syrphidae and Dolichopodidae with only a few individuals (Table 1). There were also many species of organisms that drowned in the water, such as ants, earwigs (*Forficula*), froghoppers (*Cercopis*), soldier beetles (*Cantharis*) and various species of snails. These individuals did not have a negative impact on the fauna in terms of predation as they were present due to an accidental occurrence with subsequent drowning.

Figure 2. Larval and pupal stage of *Dasyhelea* spp.

The dominant taxa

Metriocnemus eurynotus

Metriocnemus larvae were consistently present in the phytotelmata during all sampling events, reaching peak abundance with 158 individuals on the third sampling day at the end of May. Subsequently, larval abundance stabilised, but exhibited a gradual decline over time. The presence of pupae was rare (Fig. 4). Larvae displayed varying lengths throughout the season, indicating the continuous production of several generations and continuous oviposition during the observed period (Fig. 5).

Dasyhelea spp.

Individuals of *Dasyhelea*, which was particularly abundant in phytotelmata, were found in both larval and pupal stages quantitatively. In the initial phase of the field

Figure 3. Larval and pupal stage of *Metriocnemus eurynotus* (Holmgren, 1883).

Table 1. Dipteran taxa found in teasel phytotelmata

Total number of common teasel phytotelmata individuals	
Taxon	**Abundance**
Dasyhelea spp.	856
Metriocnemus eurynotus	546
Cecidomyiidae	20
Stratiomyidae	4
Syrphidae	3
Dolichopodidae	1

experiment, larvae appeared sporadically, with a gradual increase in abundance in the latter half of the season. The number growing significantly on the fifth sampling day (mid-June) and peaking on the seventh sampling day (early July, before a dry period) was 299 individuals. The number of pupae also increased, but to a much lesser extent than the number of larvae (Fig. 6). Similarly, larvae of *Dasyhelea* of varying in lengths were present throughout the season with numerous oviposition activities during the sampling period (Fig. 7).

Temporal and spatial distribution

Individuals of the second dominant species, *M. eurynotus*, were spatially distributed at lower levels throughout most of the season (Fig. 8). In the beginning, larvae were most frequently found in the lowest level A, where they reached a maximum of 117 larvae collected. On the fifth sampling date, larvae were concentrated in higher levels. During the last sampling dates, the presence of larvae considerably decreased and were found to have moved to higher E and F levels. Individuals of the genus *Dasyhelea* developed a gradual increase in population. At the beginning of the season, few larvae were present in the lowest levels A and B. On the seventh day of sampling, larvae

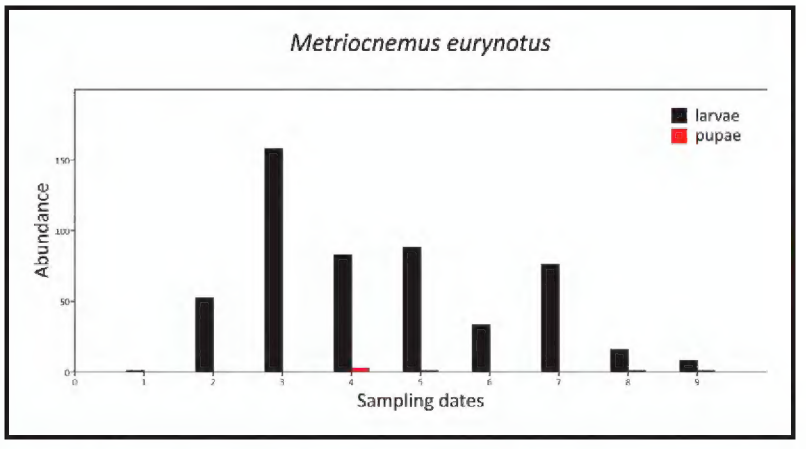

Figure 4. Temporal abundance of *M. eurynotus* per sampling period. (Black colour – larval stage, red – pupal stage).

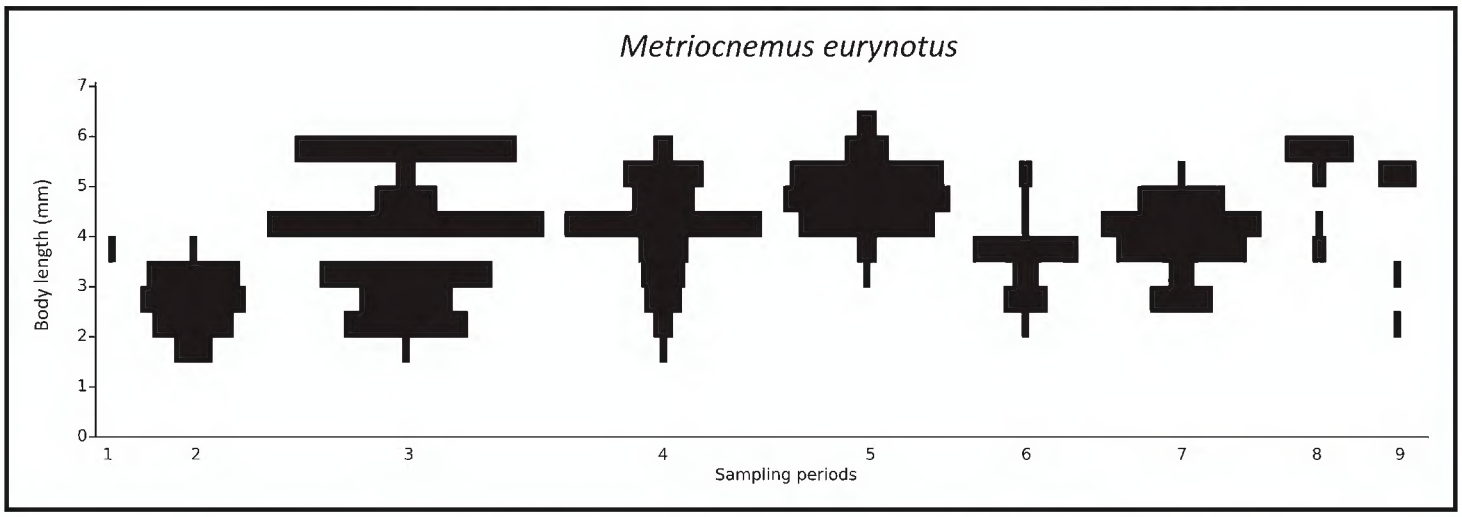

Figure 5. Frequency of *M. eurynotus* larval size groups per sampling period.

occupied almost all levels from A to F and reached a maximum abundance in level D with 136 individuals. The situation changed similar to *M. eurynotus* during later dates with the *Dasyhelea* larvae being distributed in higher levels from D to H, still in high abundance.

Dasyhelea pupae observed in motion

An unexpected result was the personal observation of *Dasyhelea* pupae actively moving between leaf axils with a thin film of water around their bodies. The pupae moved along the stems (about 20 cm) in a wavy pattern to the lower phytotelma in 3 to 4 minutes (Fig. 9). By this time, both the upper and lower phytotelma contained sufficient water to avoid the onset of drought. This was observed in the early hours of the morning at 6 am, so the water could not have been overheated.

Discussion

This study focused on the Diptera in the phytotelmata of the teasel (*D. fullonum*), recognising that flies are the predominant macroinvertebrates in these temporary aquatic habitats. A total of 1429 Diptera individuals were identified in 6.5 litres of collected water. *Dasyhelea* and *Metriocnemus* were the most common and abundant genera in the phytotelmata samples. The presence of these genera is similar to historical records from Europe (Goethgebuer 1925; Zavrel 1941; Münchberg 1955; Disney and Wirth 1982; Oboňa and Svitok 2012; Mauch and Mauch 2022; Oboňa et al. 2024) and other regions, such as Borobev (1960) from Russia, Baumgartner (1986) from USA and Siri et al. (2008) from Argentina.

Individuals of the genus *Dasyhelea* were not identified to the species level due to ambiguous differences in the larval stage (Oboňa and Dominiak 2014). It is assumed that these individuals may belong to the species *Dasyhelea bilineata* Goetghebuer,

1920 and *Dasyhelea flavifrons* Guérin, 1833. Larvae and pupae of *D. bilineata* have been documented in the water-filled leaf axils of *D. fullonum* (Dominiak and Szadziewski 2010; Mauch and Mauch 2022; Oboňa et al. 2024). *D. flavifrons* is more commonly found in temporary water-filled tree holes with a wide distribution of Holoarctic arboreal species (Oboňa and Dominiak 2014). Both species inhabit not only phytotelmata, but also other temporary habitats such as rock pools (Ronderos et al. 2006; Scharf et al. 2019), tree holes and in the sap of various tree species. All information regarding the distribution of *Dasyhelea* has been comprehensively summarised in Dominiak and Szadziewski (2010). The genus *Metriocnemus* occurs in a wide range of habitats (Sæther 1995). The species *M. eurynotus* has been recorded not only in phytotelmata, but also in other hygropetric biotopes, such as fountains (Hamerlík and Brodersen 2010), sewage filter beds (Learner 2000) and springs (Lencioni et al. 2011).

In phytotelmata sampled in this study, the initial coloniser was *M. eurynotus*. The larval abundance peak was observed on the third sampling period, at the end of May, inhabiting the lowest levels mostly. After the initial maximum, the population gradually declined. Pupae were sporadically present, with individuals of *M. eurynotus* pupating outside the aquatic environment of phytotelmata.

Dasyhelea larvae were generally absent at the beginning of the season, sporadically a few individuals appearing in insignificant numbers. Abundance began to increase after the peak abundance of *M. eurynotus*. *Dasyhelea* reached its maximum abundance on the seventh sampling period in July. Dominiak and Szadziewski (2010) confirmed the presence of *D. bilineata* larvae during the summer months. In all cases of *Dasyhelea* presence, both larvae and pupae were observed, indicating that they were not competing with each other. Kitching (1972) recorded another species, *D. dufouri* in dendrotelmata, as a more stable environment, laying eggs in summer and larvae present during the winter months with maximum in February.

The mentioned species of *D. billineata* and *D. flavifrons*, which occur in teasel, are adapted to the life cycle of the short duration of the teasel phytotelmata. Females probably lay eggs only once in their lifetime (Keilin 1921; Kitching 1972) and the

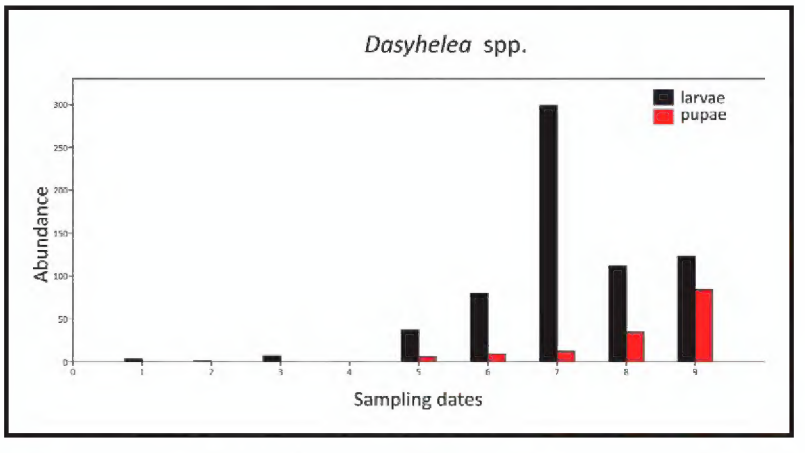

Figure 6. Temporal abundance of *Dasyhelea* spp. per sampling period. (Black colour – larval stage, red – pupal stage).

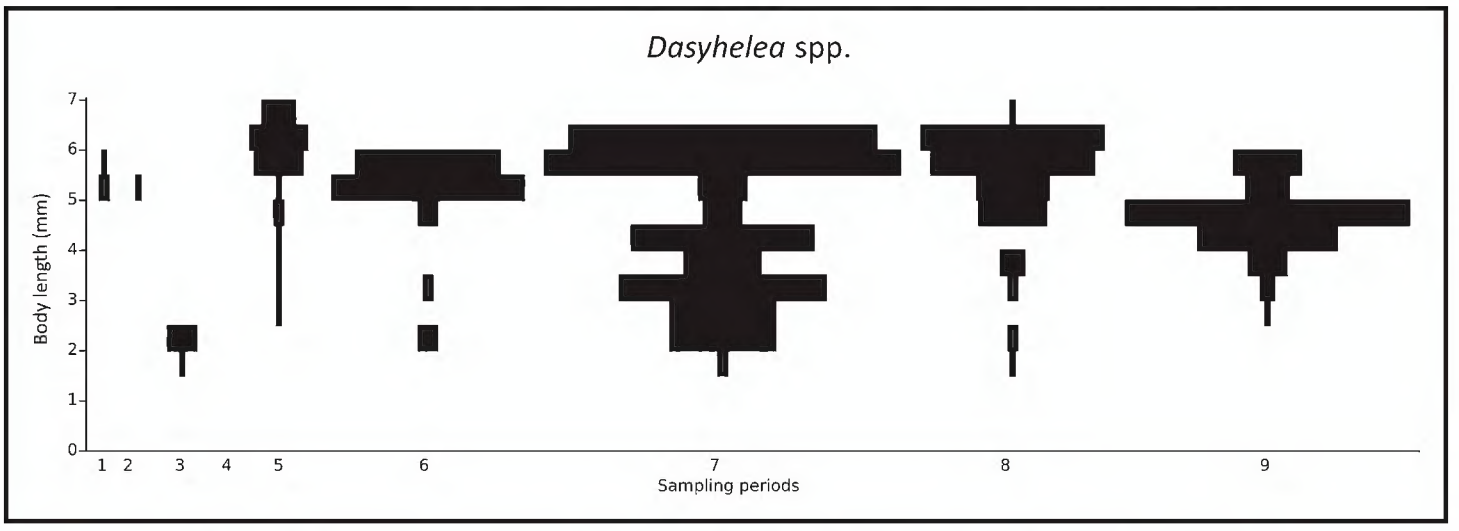

Figure 7. Frequency of *Dasyhelea* spp. larval size groups per sampling period.

life cycle is very short. Based on the sampling method, we cannot determine exact number of generations based on the length of the larvae in individual phytotelmata. However, for both *Dasyhelea* and *Metriocnemus* species, we did observe the constant oviposition activity for the establishment of a new generation. *Metriocnemus* larvae with longer body size, present already in the third sampling date, point to a short life cycle since the establishment of phytotelmata.

In this study, a maximum of eight levels of leaf axils with water and macroinvertebrates (dipteran larvae) were observed on sampled individuals of teasel. Individual levels developed gradually, with the highest positioned phytotelmata being often without water, indicating a lower volumetric capacity. At the beginning of the season, *M. eurynotus* predominantly occupied lower phytotelmata levels, achieving the maximum abundance in level A close to ground. These lower levels are characterised by greater volume and a prolonged aquatic phase, but with shorter leaf lifespan. Over time, these lower phytotelmata are usually the first to be damaged or desiccated. As a result, the *M. eurynotus* population gradually shifted to higher levels.

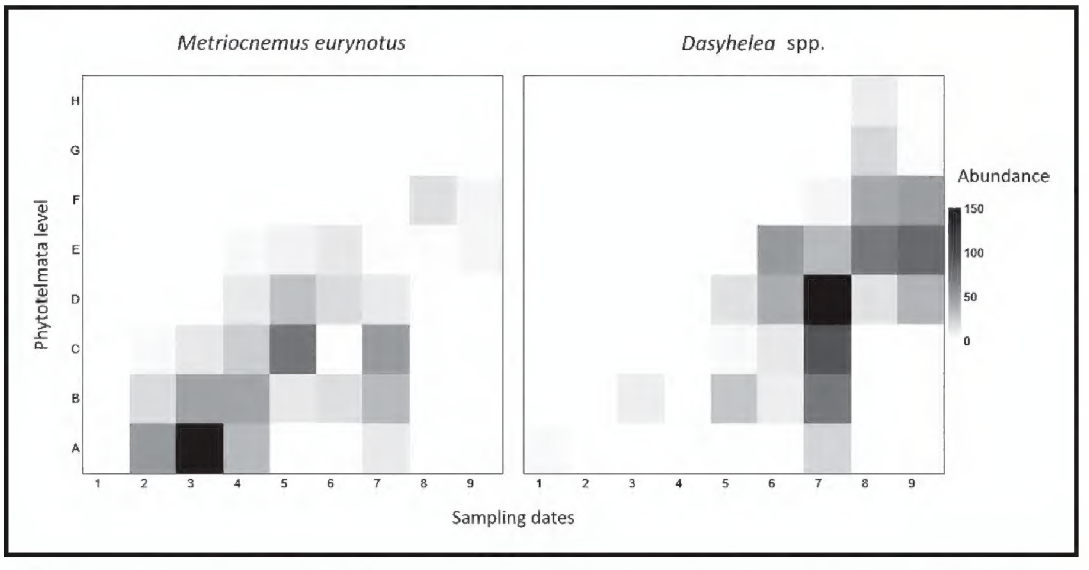

Figure 8. Temporal and spatial distribution of abundance of the dominant taxa *M. eurynotus* and *Dasyhelea* spp. in phytotelmata levels.

Dasyhelea larvae with a delayed onset used the middle phytotelmata. They were most common in phytotelmata of the levels D, but were also found in the highest observed phytotelmata. One of the prerequisites for *Dasyhelea* occurrence in higher levels may be damaged lower leaves or ability to positively respond to environmental variables compared to chironomids (Gilkey 2022).

The main conclusion is that both *M. eurynotus* and *Dasyhelea* spp. effectively colonised diverse spatial and temporal niches within the phytotelmata.

The movement of *Dasyhelea* pupae along the stems was also independently recorded on teasel at another site, 10 km away from the study plots in Kapušany (Slovakia, 49°03'12.6"N 21°20'16.3"E) a few years later in 2022. This suggests that individuals may move between different phytotelmata, thereby reducing population density by colonising new levels or finding a better place before eclosion. It also suggests that they may be able to avoid unfavourable conditions that way. Ronderos et al. (2006) claim that pupae show an important change in activity when the

Figure 9. Movement of *Dasyhelea* pupae along the stems between phytotelmata.

temperature of the water varies, with mobility increasing as the temperature rises. These suggestions require further investigation into the behaviour of *Dasyhelea* pupae.

Conclusion

This work focused on Diptera inhabitants in phytotelmata of common teasel. Based on sampling, we found the presence of *Dasyhelea* spp. and *Metriocnemus eurynotus* as the dominant taxa. Despite the unpredictable duration of the aquatic phase and also the short duration of the phytotelmata, these two taxa are able to inhabit the phytotelmata without competing with each other in space and time. While *M. eurynotus* larvae inhabited the phytotelmata throughout the whole season, mainly in the lower levels with an abundance peak at the beginning of the season, *Dasyhelea* spp. appears in the second half of the season and occupied the middle to higher levels.

In addition, the unexpected observation of *Dasyhelea* pupal mobility opens opportunities for further research on the adaptations of organisms in this ecosystem. Phytotelmata should not be perceived only as isolated islands of water. The multiple levels of phytotelmata along teasel stems provide habitat heterogeneity that allows gradients of environmental factors to be explored. Each level may have unique characteristics and studying these differences provides insights into how different factors influence the distribution, abundance and behaviour of organisms in the phytotelmata. The discovery that some organisms can move between leaf levels opens new ways of exploring and perceiving this environment. Further research is needed in this direction to clarify the principles and patterns that our new knowledge has so far only outlined.

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